

Ammospermophilus nelsoni.

By Troy L. Best, Amy S. Titus, Cynthia L. Lewis, and Katharine Caesar

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Ammospermophilus nelsoni (Merriam, 1893)

San Joaquin Antelope Squirrel

Spermophilus nelsoni Merriam, 1893:129. Type locality "Tipton, San Joaquin Valley [Tulare Co.], California."

Ammospermophilus nelsoni: Lyon and Osgood, 1909:172. First use of current name combination.

Ammospermophilus nelsoni amplus Taylor, 1916:15. Type locality "20 miles south of Los Baños, Merced County, California."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuroomorpha, Family Sciuridae, Tribe Marmotini, Subtribe Ammospermophilina (Hafner, 1984). The genus *Ammospermophilus* contains five species; *A. harrisii*, *A. insularis*, *A. interpres*, *A. leucurus*, and *A. nelsoni*. A key to the species is presented in Best et al. (1990). *A. nelsoni* is monotypic (Hall, 1981).

DIAGNOSIS. *Ammospermophilus nelsoni* (Fig. 1) differs from *A. l. leucurus* in being larger and more buffy (less grayish), and in having more widely spreading zygomatic arches (Hall, 1981). The skull (Fig. 2) is similar to that of *A. leucurus*, but longer and broader; auditory bullae are conspicuously larger, more inflated, and distinctly corrugated. The corrugations are due to the presence of two transverse constrictions, marking the position of vascular canals; they are faint or absent in *A. leucurus* and *A. harrisii*. The rostrum and nasal bones are somewhat longer, and the upper incisors and first upper premolar are larger than in *A. leucurus* (Merriam, 1893).

GENERAL CHARACTERS. The dental formula is $i\ 1/1$, $c\ 0/0$, $p\ 2/1$, $m\ 3/3$, total 22 (Ingles, 1965). The upper parts are dull yellowish-brown or buffy-clay color, as are the outer surfaces of the legs. There is a pale stripe on each side reaching from behind the shoulder to the rump. The underparts, feet, and eyelids are soiled whitish, and the feet are suffused with buffy. Above, the proximal one-third of the tail is buffy-clay color like the back; the distal two-thirds is mixed black and whitish with a whitish border. Below, the tail is soiled or buffy whitish, bordered on the distal two-thirds with a broad subterminal black band, and edged with whitish. There also is a narrow black zone at the base of the tail hairs. The upper parts are rather coarsely lined with black hairs that are absent from the legs, giving the legs a slightly different tint, and in some the ground color of the legs and sides just above the forelegs is different, being suffused with dull buffy-ochraceous (Merriam, 1893).

Diameter of the post-squamal sinus and the palatal width at the third molar exhibit secondary sexual dimorphism (Hafner, 1981). Males average slightly larger than females. Mean external measurements (in mm; range in parentheses) of males and females, respectively, are: total length, 249 (234-267), 238 (230-256); length of tail vertebrae, 73.1 (66-78), 72 (67-78); length of hind foot, 41.3 (40-44), 40 (37-43; Taylor, 1916); length of ear (dry), 8.2 (8-9), 8.5 (8-9.5; Howell, 1938); crown length of ear, 5.3 (5-6), 5.7 (5-6; Grinnell and Dixon, 1918). Mean cranial measurements (in mm; range in parentheses) of males and females, respectively, are: greatest length of skull, 42.2 (41.5-43.1), 40.1; mastoid width, 21.4 (21.2-21.6), 21.1 (20.5-21.7); interorbital constriction, 10.2 (9.9-10.5), 9.7 (9.2-10.2); and length of nasals, 12.4 (12.2-13.1), 12.0 (11.6-12.5; Taylor, 1916). Additional cranial measurements (in mm) of 12 adults (sexes combined) are: palatilar length, 18.9 (18-19); zygomatic breadth, 24.5 (23.5-25.7); cranial breadth, 19.6 (18.8-20.6); postorbital constriction, 13.8 (13.5-14.3); and length of maxillary toothrow, 7.7 (7.2-8.5; Howell, 1938). Three adult females averaged 154.5 g (141.8-179.0; Grinnell and Dixon, 1918).

Geographic variation primarily is in coloration (Taylor, 1916)

and size. Specimens from the southern San Joaquin Valley are smaller and less yellowish in coloration, with a gradual increase in size to the largest, more yellow northern forms (Hafner, 1981).

DISTRIBUTION. The San Joaquin antelope squirrel occurs in the San Joaquin Valley of California (Fig. 3; Grinnell, 1933). In addition, it occurs on the slopes and ridgetops in the foothills along the western edge of the valley, in the Cuyama and Panoche valleys, and on the Carrizo and Elkhorn plains (Kilburn and Williams, in press). The altitudinal range is from about 50 (Grinnell, 1933) to 1,100 m (Kilburn and Williams, in press).

FOSSIL RECORD. *Ammospermophilus* probably diverged in the Miocene (James, 1963). Post-Pleistocene fossils resembling *A. nelsoni* have been found near McKittrick, Kern Co., California (Schultz, 1938). *A. fossilis* was described from the early Clarendonian of the Cuyama Valley, California, and *A. hanfordi* was described from the early Blancan of Franklin County, Washington (Gustafson, 1978). *A. nelsoni* may have been isolated from *A. leucurus* by Wisconsin-age woodland in the Transverse ranges of California, with possible subsequent introgression (Bolles, 1981).

The original invasion of the range of *A. nelsoni* was over the low passes of the southern Sierra Nevada and Tehachapi mountains (Hawbecker, 1953). With return of less arid conditions at the end of the Xerothermic, the corridor between the Mojave Desert and San Joaquin Valley was closed to most desert species, and *A. nelsoni*, subjected to the severe, hot, and xeric conditions of the San Joaquin Valley, evolved in isolation from its Mojave Desert counterpart (Hafner, 1981).

FORM AND FUNCTION. Evident adaptations to the severe desert in which *A. nelsoni* evolved include pale coloration of summer pelage to increase reflectance and relatively large auditory bullae to compensate for lowered sound transmission in the dry air (Hafner, 1981). The ears do not project dorsally to the level of the head, the pinna is rounded and its width is equal to or greater than its height, and there is no antitragus or intertragal notch. The ears are



FIG. 1. Photograph of *Ammospermophilus nelsoni*. Courtesy of D. F. Williams.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Ammospermophilus nelsoni* (male, Natural History Museum of Los Angeles County 2928, from McKittrick, Kern Co., California). Greatest length of cranium is 40.4 mm. Photographs by T. H. Henry.

short and broad, the length of tail is 25–33% of the total length, and the legs are relatively long. The soles of the feet are heavily haired. The cranium is nearly quadrate. The external margins of the infraorbital foramina usually are vertical, the bases are directed ventrolateral, and the masseteric tubercles are situated ventral or slightly ventrolateral to the foramina. The zygomatic plate forms an angle of about 50° (Bryant, 1945).

Maximum length of the dorsal guard hairs is 13 mm and the width is up to 115 μ (Mayer, 1952). Autumn and winter pelage is darker and softer than the summer pelage (Merriam, 1893), and is more grizzled or spotty; hues of coloration are paler, and the white stripes on the sides are less conspicuous (Taylor, 1916). During molt, the pale, buffy-clay color of the head in summer pelage is in striking contrast with the much darker tints of the neck and back, which are completely covered with the new coat. The two are

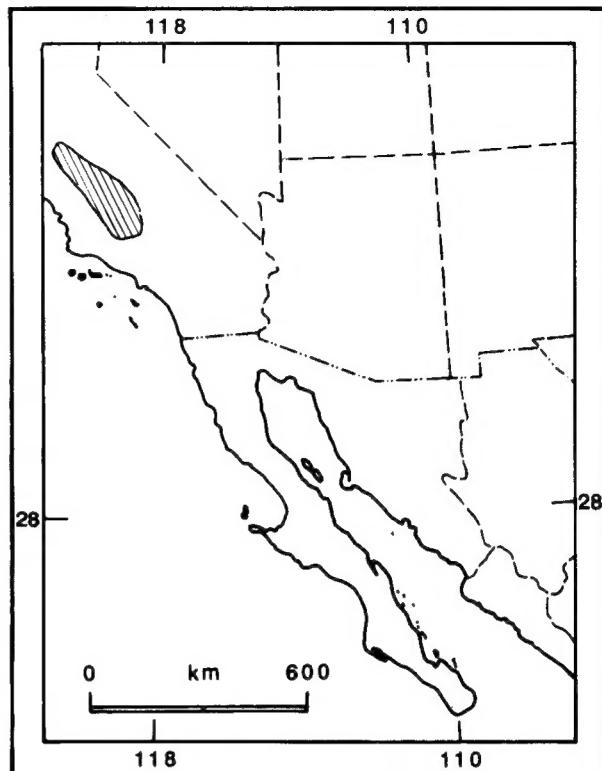


FIG. 3. Distribution of *Ammospermophilus nelsoni* in central California (Hall, 1981).

separated by a sharp line of demarcation that crosses the occiput between the ears (Merriam, 1893).

Winter molt coincides with sexual development and summer molt with regression of testes in males. After maturity and during winter or breeding-pelage phase, the scrotum is gray to black and covered with short black hair. In the immature and summer or nonbreeding-pelage phase, the scrotum is smaller, less pigmented, and may be covered with long, tawny hair. Winter pelage persists until the breeding season is completed for each sex, but completion is not simultaneous in the sexes. The coat of females does not start its molt until all duties pertaining to the young are completed, thus she molts about 1 month later than the male. Young follow the course of the female. In mid-February, both sexes show changes in the head region. In late April, males are almost completely molted, but females and young are just starting or not yet started to molt. By mid-May, the young have molted and females have most of their summer coat. The summer coat can be felt coming in beneath the winter pelage. Molting starts again in late summer; on 22 August, males had molt lines near the rump, but females were still in summer pelage. By 26 September, the posterior 50% of the body of captive females had completed the molt. On 5 October, an adult male had summer pelage on the head, while a young male had such pelage across the shoulders. By mid-October, females are about 60% molted and males 90%. Summer pelage starts at the head and works back to the tail, while winter pelage starts at the rump and works to the head. Summer pelage is sparser and paler in color than winter. This may allow better air circulation and light reflection, whereas the darker, heavier winter coat absorbs and retains heat (Hawbecker, 1975).

Hypothalamic thermosensitivity is high in *A. nelsoni*, while extra-hypothalamic core thermosensitivity is low (Heller and Henderson, 1976). The average proportionality constant relating rate of metabolic heat production to hypothalamic temperature is $-5.1 \text{ watts kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$ at an ambient temperature of 10°C , $-5.5 \text{ watts kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$ at 20°C , and $-7.3 \text{ watts kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$ at 30°C . The average threshold of hypothalamic temperature for the metabolic heat production response is 42.4°C at an ambient temperature of 10°C , 41.3°C at 20°C , and 39.1°C at 30°C (Henderson and Heller, 1976).

Mammae of lactating females are greatly enlarged and variously distributed. Of 17 females, eight had seven pairs in use; two

thoracic, three abdominal, and two inguinal. Eight had six pairs in use; two pairs in each region. One had seven on one side and six on the other; three mammae were in the thoracic region (Hawbecker, 1975).

The baculum is <2 mm in length and may act only as a hardened tip to facilitate initial intromission of the penis. The bizarre fan-shape, asymmetry, and variability in number of tooth-like projections of this delicate bone may have no other functional attributes (Hafner, 1981).

ONTOGENY AND REPRODUCTION. The breeding period is late winter through early spring (Hawbecker, 1953). Young are nearly all born in March and are first seen above ground about the first week in April. This is the only breeding season, and it coincides with the one period of the year when green vegetation is present (Hawbecker, 1958).

Usually, the testes of adult males reach their breeding condition in autumn, much before the ovaries of females begin to develop. On 3 August, one had a dark, short-haired scrotum, but no testicular development; on 22 August, each of two had a small scrotum and 4-mm testes; on 11 September, four had scrotal testes 6–10 mm in length and pigmentation; on 15 October, one had 24-mm testes; and on 27 November, two had scrotal testes 21 and 15 mm in length with the scrotum black. On 11 November, 40 days before the start of new plant growth, fully developed sperm occurred in testes and epididymes. Most males in November have testes 21–25 mm in length. The annual period of fertility is confined to the cooler portions of the year. Three had testes 18–23 mm in length on 11 November, and on 6 March, five had testes 16–22 mm; sperm were present in all of these. By the end of March, testes begin to regress in size and by mid-April most testes are 4–8 mm. This size is maintained through the summer, but occasionally some males have enlarged testes in May. Body size and length of testis are not related. In addition, all males are not reproductively active at the same time. Young-of-the-year have longer, paler hair over the scrotum than adult males, and apparently do not breed (Hawbecker, 1975).

The breeding cycle in the female is characterized by a shorter period of maximum development of reproductive organs than in the male. The cycle, however, includes care of the young, and that extends the full period to that of the male. From 15 August to 15 December, females show no external or internal development. On 22 December, one had a slightly enlarged uterus with no external change, and another showed the opposite. On 21 January, two females had enlarged or open vulvas; another showed maximum uterine development. Breeding readiness probably begins about 20 January; however, all are not ready this early. Some that are ready do not mate, and some do not develop in a given year. On 22 February, females may have fully developed mammary glands (but not lactating), vulva, and uterus, but exhibit no signs of having mated or borne young. Deviations in reproduction may be correlated with disturbance or food failure. Readiness for breeding lasts until 5 March; after this, females show signs of regression. No young are found out of the burrow in March, but most females are lactating (Hawbecker, 1975). On 30 March, one lactating female had seven pairs of mammae in use (Hawbecker, 1959).

The gestation period is 26 days. Embryos range in number from six to 11 with an average of 8.9; one had 12 fetal scars. Embryos are present in late January, but development is concentrated in February and early March. On 16 February, a female contained 54-mm embryos (Hawbecker, 1975).

A brood of seven young was nursing on 4 April when they came above the ground, but nursing apparently ceased by 20 April. On 25 April, two females appeared to have nursed recently. Weaning may be started or even completed before coming aboveground, but is in no way consistent after emergence. Young seen aboveground at the earliest date are busily gathering food. During weaning, the behavior of the female toward her young changes. The female feeds alone and leaves any young that approach her. She keeps contact by occasional visits or by using the calls by which family groups communicate. She does not allow them to nurse even though they nuzzle her from time to time. She may even spend the night in a different burrow (Hawbecker, 1975).

On 4 March, nine young in a litter had a total weight of 38 g or an average of 4.88 g at birth; two were 58 mm in length. They were hairless and if clawed, only minutely so, but were quite active and able to make mewing sounds. By 10 March, they totaled 53 g, or a gain of about 1.7 g/young. Claws were present, slight pinnae

were discernible, and hair was darkening the skin of the head; there was less mewing, but more activity. By 14 March, they weighed 61.3 g, with two weighing 6.5 and 7.3 g. One measured 70 mm with the head much darker, and a crease where the eyes were to open; all were active. On 16 March, the tail was up over the back in characteristic fashion. After 30 days, the eyes are still closed, but the young are well furred and bite when teased. Young occur aboveground about 30 days after birth; that is, beginning about 4 April. On 12 April, two young males (about 8 days after emergence) weighed 40 and 42 g. The pelage was fine and dark, but not thick or adult. On 16 April, three weighed 70.6, 70.7, and 43 g, with the last having a bad eye. The healthy ones were 183 mm in length (Hawbecker, 1975).

Juveniles have been seen on 7 and 18 May. Probably these young were born during April or earlier (Taylor, 1916). A 25%-grown male was present on 7 May and a 50%-grown male was present on 18 May. There were two that were 70% grown on 9 May; they were foraging for themselves (Grinnell and Dixon, 1918). Change from juvenile to adult pelage begins about the time they become independent, and usually by mid-May the adult summer coat is present (Hawbecker, 1975). Young are recognized by pelage, size, and sexual development. After the first year, it is difficult to tell age groups apart, unless they are marked. The usual life span is <1 year. However, several have lived in the wild for >4 years, one to 5 years 8 months. There is no difference in survival between sexes (Hawbecker, 1958).

ECOLOGY. In the southern and western San Joaquin Valley, San Joaquin antelope squirrels are inhabitants of open, rolling land and gentle slopes with shrubs; typical vegetation includes *Atriplex* and *Ephedra* (Hawbecker, 1975). Near Panoche, San Benito County, at an elevation of about 360 m, they live in habitat containing such plants as *Ephedra californica*, *Juniperus californicus*, *Gutierrezia californica*, *Poa scabrella*, *Bromus rubens*, and *Erodium cicutarium*. Rainfall averages about 12.5 cm, but may reach 25.5 cm (Hawbecker, 1958). In Kern County, they are found in hilly regions and sandy washes (Taylor, 1916). Near Los Banos, Merced County, and near Mendota, Fresno County, the habitat is devoid of brushy cover. Annual plants such as *B. rubens*, *B. mollis*, *Astragalus oxyphysus*, *Phalaris minor*, *E. cicutarium*, and the perennial *Stipa pulchra* have a short growing season. This lasts from the beginning of the rains the previous autumn until the beginning of hot weather in the spring. The rest of the year, except for *Trichostema lanceolatum* in the summer and an occasional composite in the autumn, the area is brown and dry. The terrain is rolling with rocky outcrops, and often is dissected by straight-walled dry washes (Hawbecker, 1947).

Six or eight individuals constitute a colony of average size (Taylor, 1916). However, they are not distributed evenly over their geographic range. There may be >10/ha in some areas, but generally there are <1/ha (Grinnell and Dixon, 1918). In grain fields near the base of the Tehachapi Mountains, *A. nelsoni* occurs in considerable numbers where it inhabits burrows dug in the hard adobe floor of the valley. Although reported as not being found closer than 6.5 km to the foothills surrounding the valley (Elliot, 1904), this species actually is found in moderate to high densities in the foothills on the western side of the valley (D. F. Williams, in litt.).

Ammospermophilus nelsoni has an affinity for alluvial and loamy soils (Hawbecker, 1953). Soils occupied are sandy loam or fine sandy loam; a deep, rich soil type. The slightly rolling portions are gravelly clay loam and are not occupied by as many squirrels as the bottomlands of finer-textured soils. These soils are easily dug even in the summer when they are dry (Hawbecker, 1947). *A. nelsoni* is found in greatest abundance today on soils of finer texture that are nearly brick-hard when dry. They also are common on soils of sandy and gravelly textures (Kilburn and Williams, in press).

During breeding season, burrows most often used by adult females and their newly emergent young are under some shrub such as *Ephedra* or *Atriplex*. *A. nelsoni* seldom excavates burrows; it utilizes burrows dug by *Dipodomys* (Hawbecker, 1953). Most burrows with old food caches are characteristic of burrows of *Dipodomys heermanni* and *D. ingens*. There are no characteristics that separate *A. nelsoni* burrows from those of *Dipodomys* (Hawbecker, 1947).

The sides of little gullies are selected for burrowing and often are honeycombed with burrows. The burrows are somewhat complicated with two or three passageways running into one at a depth of 30 cm or more. This passageway, in turn, may join one or two

other aggregations of entrances. Of several burrows excavated, no nests or food stores were discovered (Taylor, 1916). Burrows often enter near the bottom of washes or gullies. The entrances vary from 4 to 20 cm in diameter, the largest holes are in soft soil, and their size is affected by weathering or caving in of the soft earth. The burrows of smallest diameter are in hard, level ground at the roots of *Atriplex*. Entrances to burrows in the banks are from 15 cm to 15 m apart. These bank burrows run back in a generally horizontal direction and are interconnected to a considerable extent. Refuge burrows are: <4 m in length; shallow, <1 m in depth; and of small size, <5 cm in diameter. *A. nelsoni* does not use trails between burrows and feeding grounds (Grinnell and Dixon, 1918).

San Joaquin antelope squirrels are omnivorous and consume vegetable and animal food of many types (Hawbecker, 1953), including the dried flesh of *Dipodomys* (Grinnell and Dixon, 1918). A *Sceloporus occidentalis* was consumed by a female on 16 January (Hawbecker, 1947). *Erodium cicutarium* and *Bromus rubens* are the most important items in the diet (Hawbecker, 1953); the cheekpouch of one from McKittrick contained 744 seeds of *E. cicutarium*. However, they do not store food in their burrows (Grinnell and Dixon, 1918). In captivity, they readily take rolled oats, rolled barley, chicken mash, rabbit chow, and dog food. Flesh is readily taken and bones are gnawed. Almost any kind of greens are acceptable, but salt cakes are not touched (Hawbecker, 1947).

Types of food may depend on the time of day, what the squirrel may find available to eat, and availability of the food type for that year or that time of year. The predominant item in the diet from December to mid-April is green vegetation, which includes *E. cicutarium*, *B. rubens*, *E. californica*, *Trifolium*, *A. oxyphyllus*, *Eremocarpus setigerous*, and *T. lanceolatum*. Insects make up >90% of the diet from mid-April to December. No specific selection of insects is obvious, but occurrence in stomachs depends on availability. Decapitated and partly eaten Coleoptera of several species occur around burrows almost any time of the year. Insects consumed include Jerusalem crickets (*Stenopelmatus longispina*), camel crickets (*Ceuthophilus californicus*), June beetles (*Phyllophaga errans*), grasshoppers (*Oedaleonotus enigma*), harvester ants (*Pogonomyrmex*), and tenebrionid beetles (*Eleodes*). Seeds usually comprise about 10% of stomach contents, except from March to May and in December and January when they may reach 20% of the diet. Seed material is a chewed up, pasty mass in almost every stomach during each season of the year. The seeds are mostly *E. cicutarium*, *B. rubens*, and *E. californica*. *Ephedra* seeds are taken green and dry; these are picked off the shrub in the spring and picked up dry in autumn at which time husks commonly are found around burrows. Young may gather food from the husks around burrows when other food is scarce. Sprouted seeds from surface caches by *Dipodomys* are dug, apparently for the seed rather than the shoot. Any palatable seeds will be taken, but those most easily obtained are most commonly used. Seeds apparently are not the favorite food, but serve as a dietary stop gap; they reach their highest percentage in the diet when the more easily gathered green vegetation or insects are less abundant. They appear to select both green vegetation and insects more often than seeds, even when seeds are abundant. This may be due to the water content of green vegetation and insects. Vertebrates are present at low percentages throughout the year, and include rodents, lizards, and their own kind. During summers, when grasshoppers are absent and *A. nelsoni* is forced to subsist mostly upon seeds, almost the only insects present in numbers are harvester ants (*Pogonomyrmex*), which are then found in the diet. This indicates a need for such material, possibly for the moisture present (Hawbecker, 1975).

The home range of both sexes is about 4.4 ha, with areas of concentration within this range. Most are always observed within this area, whether over a period of a few months or several years. There are exceptions, however, where both sexes and both young and adults make long moves. These moves are not correlated with the breeding season. The longest move on record was by an immature male that moved 1,260 m. The longest by a female (adult) was about 900 m. These moves may be due to population pressure or changes in food supply. During 3.5 h, one *A. nelsoni* made a circuit of 375 m. From one end of this range to the other was 120 m. The range was about 240 m in diameter and 4.4 ha in area. Only 50% of its homerange or less is covered each day (Hawbecker, 1958).

Immigration of *Spermophilus beecheyi* may crowd out *A. nelsoni* and has served to restrict its range (Taylor, 1916). *Dipod-*

omys also may exert an influence, as their burrows are used by *A. nelsoni* almost to the exclusion of building any of their own. It seems possible that the range of the squirrel may be determined, at least to some degree, by the range of *Dipodomys* (Hawbecker, 1953).

Horned larks (*Otocoris alpestris*) feed and nest in the same areas as *A. nelsoni*. During their nesting season they chase and pick at *A. nelsoni*, indicating that the squirrels may bother their nests. This bird and the white-crowned sparrow (*Zonotrichia leucophrys*) serve as "lookouts" for the squirrel. When these birds are disturbed and give their alarm notes, the squirrels listen closely. It is impossible to stalk the squirrels when the birds are present. Loggerhead shrikes (*Lanius ludovicianus*) will chase *A. nelsoni* (Hawbecker, 1953). *A. nelsoni* also occurs with the mammals *Thomomys bottae*, *Chaetodipus californicus* (Hawbecker, 1951), *Taxidea taxus*, *Canis latrans*, *Mustela frenata* (Morrell, 1972), *Sylvilagus audubonii*, *Lepus californicus*, *Perognathus longimembris*, *P. inornatus*, *Dipodomys heermanni*, *D. ingens*, *D. nitratoides*, *Onychomys torridus*, *Neotoma lepida*, *Vulpes macrotis* (Hafner, 1981), and *Peromyscus maniculatus* (Boolootian, 1954), and with the reptiles *Phrynosoma platyrhinos*, *Gambelia silus*, *Uta stansburiana*, *Sceloporus occidentalis*, *Cnemidophorus tigris*, *Coluber constrictor*, *Pituophis melanoleucus*, and *Crotalus viridis* (Morrell, 1972).

Taxidea taxus is an important predator of *A. nelsoni* and excavates many of its burrows. *C. latrans* and *V. macrotis* also dig up burrows of *A. nelsoni* and probably capture some individuals (Grinnell and Dixon, 1918), but *A. nelsoni* is not an important part of their diet (Hawbecker, 1943, 1953). *M. frenata* and *Lynx rufus* occur in the same range, but there is no evidence that they are significant predators of *A. nelsoni*. A pellet from a red-tailed hawk (*Buteo borealis*) contained fur of *A. nelsoni*. Pellets from burrowing owls (*Speotyto cunicularis*) did not contain remains of this species (Hawbecker, 1953), but pellets from other owls (*Bubo virginianus* and *Tyto alba*) occasionally contain remains of *A. nelsoni* (Tappe, 1941). The prairie falcon (*Falco mexicanus*) also is a potential predator (Hawbecker, 1951).

Human activity is the greatest threat to *A. nelsoni*. Because of cultivation of the land, it seems only a question of time until the eventual extermination of this species (Grinnell and Dixon, 1918). Because of intense agricultural development of the San Joaquin Valley, beginning with the draining of Tulare Lake (about 1900) for irrigation of the valley floor, *A. nelsoni* has been subjected to extreme destruction of its habitat. No extant populations occur north of the old Tulare Lake shoreline. While small populations may still exist, it is probable that *A. nelsoni* will soon persist only on the dry southern plains on the southwestern end of the valley (Hafner, 1981). It is listed as threatened by the state of California (Kilburn and Williams, in press).

Ammospermophilus nelsoni will not occupy cultivated land (Grinnell and Dixon, 1918) or natural areas surrounded by cultivated land (Hawbecker, 1947). These squirrels were quite abundant on three sides of an extensive alfalfa field that was entirely surrounded by tracts of *Atriplex*, yet none entered this field or touched a leaf of alfalfa. However, they occurred between barley fields and their cheekpouches contained barley grains (Grinnell and Dixon, 1918). Because *A. nelsoni* often occupies barren soils that have no agricultural importance, the possibility of its doing damage by burrowing through the walls of irrigating ditches or by eating the seeds of cultivated plants is remote. Therefore, it is of little or no economic importance (Taylor, 1916).

Ammospermophilus nelsoni will enter any trap into which it can fit, including can-traps it has to squeeze into. Usually, it approaches the trap with some caution. All bait around the trap is picked up, and even some tunneling under the trap may be started. If the trap is accidentally sprung, then tunneling may be so extensive as to dislodge and make available all of the bait. Usually, the trap is entered; the quickest path to the food is taken. Rolled oats is the best bait throughout the year, even during spring when there is an abundance of green vegetation (Hawbecker, 1958).

The toe-removal method of marking does not seem to affect them adversely; one newly marked *A. nelsoni* re-entered the trap 40 min after being marked, another in 1 h, and several within 2 h. There is no evidence of permanent disability, as marked animals show up consistently for months and years. However, most marked *A. nelsoni* are not recaptured the following year. This may indicate decreased fitness of marked animals or natural attrition (Hawbecker, 1958). Recent studies have revealed that >80% of the animals

trapped and marked were never recaptured, although they were observed in the area for up to 3 years after capture. Most animals were extremely trap-shy after an initial capture and readily learned how to steal bait from traps without being recaptured (D. F. Williams, in litt.).

San Joaquin antelope squirrels move about very little in the cold, but even less in the heat (Hawbecker, 1953). When exposed to a temperature of 31–32°C in the hot sun (thermometer in the shade), they die. When exposed, their actions soon become frenzied and a frothing at the mouth occurs that may be a type of perspiration. Convulsions take place followed by rapid slowing of activity, and death ensues. Once this cycle has started, removal to shade and cooling the body does not save the animal. On 26 June, this was observed at a shade temperature of 32°C, but surface temperature was 45.5°C and relative humidity was 6%. Temperatures 60 cm underground were 4.7–5.7°C less than the shade temperature, and the relative humidity was 33%. Occasionally, a squirrel ventures out in the hot sun, but only for a short time. There is little activity during the heat of the day. There is no evidence of aestivation or hibernation. So few adults are observed in comparison to numerous young that dormancy seems indicated, but that is not the case (Hawbecker, 1958).

Cold does not bother the squirrels as much as heat. They survive in their burrows when surface temperatures are below 0°C with no apparent effects. Young of about 40 g will die on cool nights when confined without food. Generally, they are not out of the burrows at temperatures <10°C unless feeding during a prolonged cold spell (Hawbecker, 1958).

Survival is largely limited to the year in which an individual is observed. During a 7-year period, 240 were marked. Of these, 193 were not captured again >9 months after their first capture. This suggests that 80% of the animals do not survive to the next year. Survival through summer is clearly the critical period. Of 29 animals captured after 1 year, only 12 were caught after 2 years. This indicates a mortality of 60% in established adults. The summer period may be coupled with a winter period nearly as critical. The heat of summer forces them to forage early in the morning and late in the evening, and although there may be plenty of food in the form of seeds, this also is the foraging time of many of the predators. During winter, there may be sufficient food present, but cold, foggy, or windy days cause difficulty in feeding. Each condition has its restrictions, but the greatest mortality occurs during the summer period, or at least before the green growth starts the following winter (Hawbecker, 1958).

Availability of a large quantity of food may aid in survival by reducing the amount of time necessary to forage, whether winter or summer. The winter season of 1951–1952 was wet and warm, a combination that resulted in heavy growth the following spring. Trapping in autumn of 1952 and early in 1953 showed that where eight squirrels a day had been usual, this year it was possible to capture 18/day. A total of 70 animals was captured; however, in February 1954 only 20 of these still survived. This was about a 70% loss by the next breeding season (Hawbecker, 1958).

San Joaquin antelope squirrels are infested, as adults, with ectoparasites and endoparasites. Fleas are also found at the mouths of well-used burrow openings. Both young and adults work dust through the hair, which possibly helps to discourage ectoparasites. The young do not become flea-laden until well furred, which is about the sixth week. Though present in adults, young-of-the-year do not have the following endoparasites: the cestode *Hymenolepis citelli*, the nematodes *Spirura infundibuliformis* and *Physaloptera spinicauda*, and the acanthocephalan *Moniliformis dubius* (Hawbecker, 1959). Ectoparasites include the flea *Diamanus montanus*, *Echidnophaga gallinacea*, *Hoplopsyllus anomalus*, *H. glacialis*, *Merengis parkeri*, *Monopsyllus wagneri*, and *Thraassis augustsoni* (Hardy et al., 1974b) and the tick *Ixodes* (Hawbecker, 1959).

Laboratory-confirmed evidence of plague (*Yersinia pestis*) has not been detected in *A. nelsoni* (Nelson, 1980). When inoculated subcutaneously with approximately 1,000 plague-forming units, *A. nelsoni* was partially susceptible to infection. It also is susceptible to laboratory-induced Buttonwillow virus (Hardy et al., 1972). Neutralization tests of serum were negative for St. Louis and western equine encephalitic viruses (Howitt and Van Herick, 1942). However, *A. nelsoni* does have a low incidence of western equine encephalomyelitis, St. Louis encephalitis, Powassan virus, and Modoc virus, but Rio Bravo virus has not been detected (Hardy et al.,

1974b). It is readily infected by subcutaneous inoculations of western equine encephalomyelitis virus. However, the infection is clinically inapparent. Long-term survival of this virus in inoculated animals has not been demonstrated. Apparently, *A. nelsoni* is not important as a natural host of this virus; it is susceptible to infection and develops antibodies, but serologic surveys rarely reveal evidence of infection (Hardy et al., 1974a).

BEHAVIOR. San Joaquin antelope squirrels are active early or late in the day and are considerably less diurnal than *A. leucurus* (Elliot, 1904). They are not early risers, rarely being found above-ground until well after sun-up. In mid-May, they first appear at burrow entrances in steep banks of gullies from 0800 to 0815 h. They appear earlier in the day here than elsewhere in the vicinity, because the bank first receives the full force of the early morning sun. The greatest activity is at 1000 h. They disappear each day between 1130 and 1200 h and rarely are seen again until 1430 h, when they begin to reappear in the shade of certain dense-foliaged *Atriplex* that grow on the brink of the wash. Although frequently seen basking during early morning sunshine, they shun direct sunlight at mid-day. As early as 1000 h, one female sought shelter in the shade of a fencepost (Grinnell and Dixon, 1918). During the hot months from May to September, early morning and late evening are the foraging times that enable them to avoid the heat. Adults may become fat in late spring and disappear during the hot months. Conversely, the young do not have the advantage of maturity and fat at this time, so are out at every suitable moment getting enough food to enable them to maintain their rate of growth over the summer (Hawbecker, 1947).

During the cool of the morning they are not active; they appear only after it becomes quite warm (Taylor, 1916). *A. nelsoni* is largely active at temperatures between 10 and 32°C (Bradley, 1967). The days and hours they are active depend on weather conditions more than the month of the year. During cold periods of the year, mid-day is used for above-ground activities, and during the warm periods the early morning and late afternoon hours are used. They seem to get as much food as possible and return to the burrow to get out of heat or cold. Days with moderate temperatures are favored, with above-ground activities occurring in a more leisurely fashion. On these days, they spend little time in the burrow and may cover a circuit of several hundred meters. Cloudy days are not favored by surface activity. Wind is not tolerated except on warm days, when surface feeding is made more bearable by the breeze. There is little activity on cold and wet days, but they may continue to feed during light rains (Hawbecker, 1953).

San Joaquin antelope squirrels are cautious about coming out of their burrows; they never come out hastily. First the nose and then the eye will stealthily appear, and then a thorough look around for possible danger is taken before they will leave the burrow. When they move, their actions are sudden, as though they had been undecided as to what to do. They are more easily alarmed by sound than by sight. An observer can walk within 10 m of them in plain sight in the open, as long as no violent motions are made. By approaching slowly and directly toward the squirrels, it is possible to get within 3 m when they are sunning themselves at the entrance to the burrows. Their sense of smell plays an important role in detecting danger, locating food, and interactions between individuals (Grinnell and Dixon, 1918).

As in other *Ammospermophilus*, the alarm call is a trill (Bolles, 1981). Call notes of *A. nelsoni* are not loud and actually are indicated more by the associated convulsive movement of the body than by the sound itself (Taylor, 1916). The calls are short with a broad band of frequencies at the onset termed a "kuk." *A. nelsoni* has a shorter pulse duration than any other species of *Ammospermophilus*, and is noticeably deeper-pitched than all but *A. interpres*. The short, harsh trill of *A. nelsoni* appears to be adapted to closed habitats. Mean values of characters of alarm calls are: length of call from first sound emitted to end of call, 1.05 s (range, 0.37–2.34); frequency band around trill at onset of call, 6.99 kHz (1.00–7.80); mean pulse duration, 0.032 s (0.022–0.038); frequency of main sound energy of the trill one-half way in its duration, 1.09 kHz (0.70–1.80); cascade ratio, 1.30 kHz (0.92–1.60); lowest frequency emitted, 0.07 kHz (0.00–0.50); frequency of the fundamental, 1.05 kHz (0.60–1.60); frequency of trill at beginning, 1.33 (1.00–2.17); frequency of first harmonic above main sound energy, 2.70 kHz (1.60–3.30); and length of trill from first clearly configured pulse

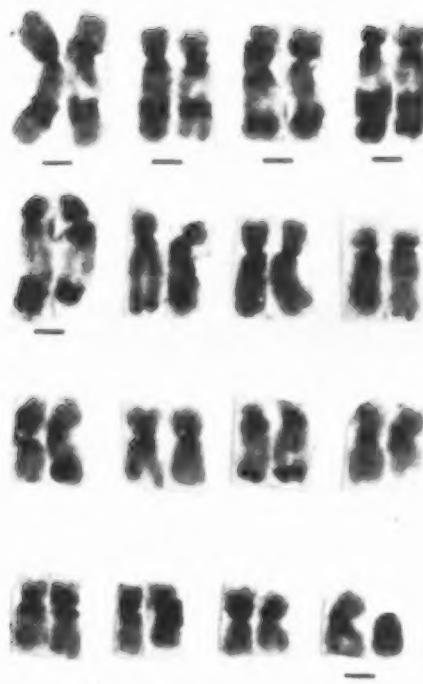


FIG. 4. C-banded karyotype of *Ammospermophilus nelsoni*. Pairs containing heterochromatic blocks (other than centromeric) are underscored. The X and Y chromosomes are the first and second members, respectively, of the right-most pair in the bottom row (modified from Mascarello and Mazrimas, 1977).

to end of call, 0.96 s (0.37–1.60; Bolles, 1988). Ontogeny, sex, temperature, or season do not affect call characters. Duration of call, band of frequencies emitted at onset, frequency of the fundamental, and lowest frequency are highly correlated with measures of the rostrum (Bolles, 1981).

When encountered, San Joaquin antelope squirrels usually are scurrying rapidly across open places between clumps of *Atriplex*, or standing straight up to their full height just before they disappear into their burrows. The normal mode of travel is by a series of short, rapid jumps of from 15 to 30 cm. When leisurely approaching a burrow, or when foraging, they sometimes slow down to a walk. The tail is the most conspicuous feature of the animal. When running, they curve the tail forward over the back, in which position the creamy undersurface is most effectively displayed so that at a distance one receives the impression that merely a bit of thistledown is blowing along over the sand. The body of the animal, with its ground-like tone of color, practically disappears. This illusion is furthered by the twitching of the tail and by the momentary pauses that closely correspond to the usual interrupted flight of a tuft of thistledown. When the squirrel is foraging on all four legs or sitting up, the tail is held curved forward over the back; rarely is the tail held in any other position. At such times, the tip of the tail often is curved slightly upward or outward. When excited or frightened, the tail is twitched rapidly fore and aft, but rarely sideways (Grinnell and Dixon, 1918).

When foraging, they move close to the ground, often stopping in the shelter of a bush or pausing in the open searching quietly, with body extended, for small seeds. They may feed while standing erect (Grinnell and Dixon, 1918). *A. nelsoni* has a route that is covered during foraging; along the route are a number of burrows that it feeds around and that it runs into if danger threatens. In one instance, an *A. nelsoni* was seen to drive a *Dipodomys* out of a burrow (Hawbecker, 1953). *A. nelsoni* travels from burrow to burrow and from bush to bush, often going around in a circle. During winter, the area covered is larger than in summer (Hawbecker, 1947).

San Joaquin antelope squirrels do not stay long in one place, but move rapidly from refuge to refuge, peering about and sampling. Sometimes grazing takes place, where the food is sampled and then when found to be acceptable, the material is bitten off directly (Hawbecker, 1975). Rarely do they pick up or even touch food they

have no interest in. One day an item may be sought out; the next it may be completely ignored in favor of some other food. Generally, they approach only far enough to smell the item before moving on to search for something of greater appeal (D. F. Williams, in litt.).

On 16 April, a non-breeding female and a non-breeding male had well-filled cheekpouches of 1.0 and 4.1 g, respectively, and empty or nearly empty stomachs, which would indicate that they do not eat while foraging. The seeds (*E. cicutarium*) had the outer husks removed, indicating that this was done en route. It appears that they gather the food and then eat it in a safe place. Insects, green vegetation, and *B. rubens* seeds seldom have been found in cheekpouches, making it appear that they are eaten at once or carried to the retreat (Hawbecker, 1975). The cheekpouches are extremely thin so the contents can be determined without taking them out. Thus, it is easy to see why insects or long, sharp seeds might not be easily carried in them (Hawbecker, 1947).

To gather green seeds of *Ephedra*, they climb into the shrubs. They show great agility in climbing and catch grasshoppers by leaping with the insect until both come down at the same place at the same time. A beetle was caught as the squirrel ran along on its hind legs and pawed the air until it hit the low-flying insect; another was caught by a sudden pounce. A group of three young *A. nelsoni* used grasshoppers for food and discarded the large legs in a heap around the mouth of their burrow (Hawbecker, 1947).

On 16 and 22 April, young were observed being pushed away by the mother, who would not let them nurse. Green material was rapidly drying by this time and the mother spent her entire foraging time away from her family, constantly eating (Hawbecker, 1947). In captivity, one female killed her young and partially ate some of them and other females ate their young shortly after birth (Hawbecker, 1975).

In nature, they do not live close to a source of water. However, they readily accept water in the laboratory. They have been kept for 7 months in the shade during hot weather without water; they appeared sleek and in no way emaciated (Hawbecker, 1947). Often they stretch out to their full length and roll over and wallow in the fine powdery alkaline dust that may be 3 cm deep along the overhanging banks of the washes. These dust baths are frequently indulged in with considerable satisfaction (Grinnell and Dixon, 1918).

San Joaquin antelope squirrels are social (Grinnell and Dixon, 1918). When removed from their territory for an extended period of time or when released in an unfamiliar area, they appear helpless and bewildered (Hawbecker, 1947).

GENETICS. The C-banding pattern of *A. nelsoni* (Fig. 4) has three autosomal pairs with large interstitial blocks of constitutive heterochromatin (Mascarello and Bolles, 1980), plus three pairs with large blocks located at the ends of their long arms. The X chromosome is larger than the Y (Mascarello and Mazrimas, 1977).

In diakinesis and diplotene cells, no cells show terminalization of chiasmata that has progressed through regions that appear to be large blocks of heterochromatin. While the failure to terminalize occurs in every diplotene region and stage of diakinesis, the situation in the asynaptic pachytene regions is not as clear. Asynaptic regions are not found in *A. nelsoni* (Mascarello, 1980).

Ammospermophilus nelsoni has a double albumin and *A. leucurus* has a single albumin (Johnson, 1968). Electrophoretic data indicate relatively low levels of genetic divergence among species of *Ammospermophilus*, with a mean Nei genetic distance measure of $D = 0.05$. *A. nelsoni* ($D = 0.053$) and *A. interpres* ($D = 0.086$) are the most distinct (Bolles, 1981).

REMARKS. Analyses of allelic frequencies at 23 loci indicate that *A. interpres* was the first of the five extant species to diverge; *A. nelsoni* was the next (Hafner, 1981). Based upon similarities of antipredator vocalizations, *A. nelsoni* is more similar to *A. interpres* and *A. insularis* than to *A. leucurus* or *A. harrisii* (Bolles, 1988). Phenetic clustering of cranial and postcranial skeletal morphology reveals that *A. nelsoni* is more similar to *A. leucurus* than it is to *A. interpres* and *A. harrisii* (Hafner, 1984).

Ammospermophilus is derived from *ammos* referring to sand, *spermatos* alluding to seed, and *philos* meaning loving or desiring affinity (Jaeger, 1955). The specific epithet *nelsoni* refers to E. W. Nelson. The common name assigned to this species in the original description was "Nelson's spermophile" (Merriam, 1893). Other common names include Nelson antelope ground squirrel, Nelson spermophile, and antelope chipmunk (Grinnell and Dixon, 1918).

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Editors of this account were DON E. WILSON and KARL F. KOOPMAN. Managing editor was DON E. WILSON.

T. L. BEST, A. S. TITUS, C. L. LEWIS, AND K. CAESAR, DEPARTMENT OF ZOOLOGY AND WILDLIFE SCIENCE AND ALABAMA AGRICULTURAL EXPERIMENT STATION, 331 FUNCHESS HALL, AUBURN UNIVERSITY, ALABAMA 36849-5414.